THE SEGMENTAL ORGAN OF PODARKE OBSCURA.

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In 1892 Goodrich[1] described "A New organ in the Lycoridea." A ciliated organ found on the dorsal side of the body, paired in every segment except the first and last few. The nephridium was found to be a well-developed organ, opening into the body cavity by a ciliated nephrostome. The narrow and tortuous character of the nephridial tube made it impossible to conceive of its acting as a genital duct considering the large size of the eggs. A comparison of the dorsal ciliated organ with the genital funnels of the capitellids described by Eisig — however, suggested the idea that the dorsal ciliated organ might function as a genital funnel. Goodrich could discover no external pore, nor was he able to observe the discharge of the genital products. Yet he considered it possible that the external pore might be formed only at maturity.

In the spring of 1905, Professor Wilson suggested that I examine this question by the study of sexually mature individuals of *Nereis* and at the same time work out the method of the discharge of its sex products. *Heteronereis* material, found in abundance at Woods Hole, was collected in the summers of 1905 and 1906 but no definite result was obtained on this form. In the case of *Podarke obscura*, however, I had better success, and although the results conform in general to the work of Goodrich on other members of the family Hesionidæ, yet they may be sufficiently different in detail to warrant their description.

The material was collected in July and August, 1905, and in June and July, 1906. Mature females were fixed before the time of discharge (which takes place regularly between 7–9 p. m.),[2] during the period of discharge, and after the eggs had been passed out from the body. Immature specimens, collected in

[1] Goodrich, E. S., "On a New Organ in the Lycoridea and on the Nephridia in *Nereis diversicolæ*," *Quarterly Journal of Microscopical Anatomy*, 1892–3, vol. 34.

[2] Treadwell, A. L., "Cytogeny of *Podarke obscura*," *Journal of Morphology*, 1900–1, vol. 17.

June were fixed as well as males obtained throughout the season. Flemming's fluid and sublimate-acetic were found to be the best fixatives. The material was then sectioned and stained in iron hæmatoxylin.

I wish to thank Professor Wilson who suggested the work and under whose direction it has been completed. Thanks are also due Professor Treadwell and Dr. McGregor for their aid in collecting material.

The nephridia of *Podarke* are present in pairs in every segment of the body except the first few. A general cross-section of the body (as is seen in Fig. 1) shows a fairly typical annelid struc-

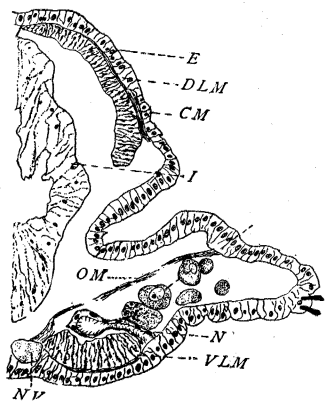

FIG. 1. × 115. A partly diagrammatic transverse section of body. *E*, ectoderm; *D.L.M*, dorsal longitudinal muscle; *C.M*, circular muscle; *I*, intestine; *O.M*, oblique muscle; *V.L.M*, ventral longitudinal muscle; *Nrv*, nerve; *N*, nephridium. (The inner end corresponds to the cavity seen in Figs. 2 and 3.)

ture, *i. e.*, the outer layer of epithelial cells, a thin layer of circular muscles, and two pairs only of longitudinal muscles, a ventral and a dorsal pair. In such a section the nephridium is found following the dorsal surface of the ventral longitudinal muscle band. It is a simple tube with practically no convolutions, opening to the exterior laterally on the ventral surface, at outer limit of the ventral longitudinal muscles. (This opening is definitely shown in Fig. 4, the transverse section did not pass through the opening.) The nephridium extends along the upper surface of the muscle, then bends diagonally inward in the segment toward the median plane and forward toward the anterior dissepiment

where it unites with a large ciliated organ in the next anterior segment. (This union is shown in Figs. 2 and 3.) The walls of the nephridium are thin, its cells contain numerous excretory particles and its cavity is lined with fine cilia. The organ receives its blood supply from branches of a ventral longitudinal blood vessel. The position of the blood vessel is shown in the sagittal section, Fig. 2. The organ as a whole is simple in structure and may be regarded as a more or less degenerate condition of the nephridium as seen in *Hesione pantherina*, the nephrostome in the latter being replaced by the ciliated organ.

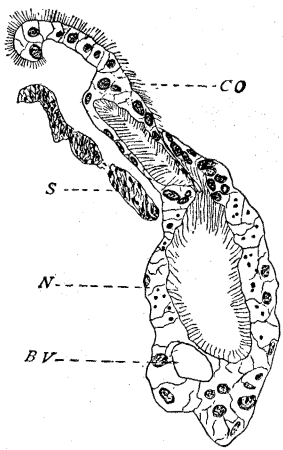

FIG. 2. × 500. A sagittal section of the segmental organ. Showing the relationship between the ciliated organ and nephridium. *C. O*, ciliated organ; *S*, septum; *N*, nephridium; *B. V*, blood vessel.

The ciliated organs of *Podarke*, like the nephridia, are paired in every segment behind the pharynx. The organ is a thin, flat, more or less triangular plate of ciliated cells, one layer in thickness, which stretches out into the body cavity anteriorly away from the dissepiment with the distal edge of the organ, or the base of the triangle turned toward the intestine and the apex of the triangular mass attached to the nephridium. The dorsal edge of the flat plate is rolled over toward the dissepiment. At the posterior edge it is often compressed and folded, but gradually broadens out into a large lip at the distal end. The ventral portion is only slightly rolled and in this case the turn is away from

the dissepiment. This fold is present only at the distal anterior end of the ventral edge where it forms a short lip.

Immature specimens show the ciliated organ lying directly on the dissepiment, from the cells of the peritoneal covering of which it develops. In mature forms the organ does not lie against the dissepiment except at the point of union with the nephridium. In a sagittal section (Fig. 2) the organ is raised from the dissepiment. Although consisting of only one layer of cells, it may be folded in such a way as to give the appearance of more than one layer. This condition is seen in Fig. 2; if it were not compressed, it would have the appearance of the organ as seen in Fig. 3.

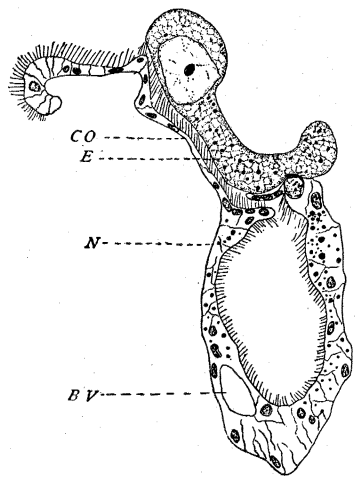

FIG. 3. × 500. A sagittal section of the segmental organ showing an egg passing along the ciliated surface. *C. O*, ciliated organ; *E*, ovarian egg; *N*, nephridial sac; *B. V*, blood vessel.

The ventral lip is not shown in either of the sagittal sections as they passed through the union of the nephridial tube and ciliated organ, whereas the ventral lip which is short and found only at the anterior edge (as has been stated), would appear in earlier sections in the series.

I have not found any indication of an internal termination of the nephridium other than the ciliated organ, and it seems evident that the latter forms an open cœlomic funnel. Its nature may best be considered after an examination of its relation to the discharge of the sex products.

In commencing the work, the material at first showed the nephridia to be so small that it seemed impossible that the large eggs could pass out through them. Goodrich's supposition that the eggs might pass to the outside through a break in the body seemed at first to be confirmed in some of my sections. I found cases where there appeared to be a definite rupture in the center of the ventral longitudinal muscles. This interpretation, however, was proved false, first by the fact that the eggs passing through the rupture were immature, ovarian eggs, whereas, in general, the eggs have been found to form their first polar spindle before leaving the body, and second, by the discovery of eggs passing along the ciliated organ and down into the nephridial cavity (Figs. 3 and 4). The walls of the nephridium are thin, but elastic and are capable of great expansion at the time of maturity. The inner end of the tube swells as the eggs become matured.

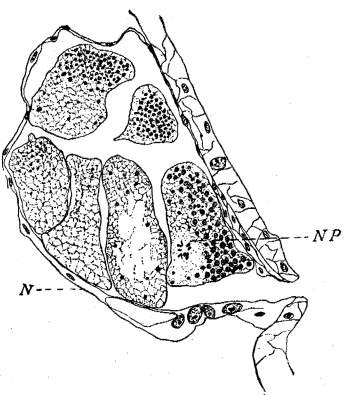

FIG. 4. × 500. A sagittal section of the nephridial sac showing the external opening at the lower end. *N*, nephridial sac; *N.P*, nuclear plate showing that the first maturation spindles are formed before the eggs are extruded. All of the eggs are in the same stage of development, the nuclear plates being visible in different sections.

(The beginning of this is shown in the nephridium in Fig. 1.) Finally the whole tube is distended and has the appearance of a large irregular sac filled with sexual products (Fig. 4). The eggs may pass into the nephridium before forming the polar spindles which are formed in that case, while the eggs are in the nephridial sac. This was probably the case in Fig. 4, or as has been

observed by Treadwell,[1] the spindles may be formed after the eggs have passed out of the body; but, as a rule, the first spindle appears while the egg is free in the body cavity, before its passage into the nephridial cavity. In the male, the relations between the nephridium and ciliated organ is the same as that in the female, but the discharge of the spermatozoa was not observed.

Goodrich[2] in his summary of the most important facts resulting from his study of the Hesionidæ, says: *Hesione sicula* has a nephridium, which opens ventrally to the exterior, passes inwards and forwards, becomes considerably coiled, and finally ends just in front of the intersegmental region by a small, simple, funnel opening into the cœlome of the next segment. Connected with the lip of the nephrostome by a narrow strip of epithelium is a large crescentic genital funnel (ciliated organ), the ciliated surface of which is marked by deep grooves. Those of the middle region converge towards the loose extremity of the organ, where it is connected with the nephrostome and with the body wall. The exact mode of exit of the genital products is unknown.

In *Tyrrhena*, the nephridium is essentially the same but the genital funnel is smaller and more closely connected with the nephrostome.

In *Kefersteinia* and *Ophiodromus* it completely surrounds the inner extremity of the nephridium.

Finally in *Irma*, where the nephridium is no longer coiled, the large genital funnel surrounds and fuses completely with its inner end, forming a trumpet-shaped cœlomic funnel. The genital products, collected together by the action of its ciliated surface pass down into the nephridium and so to the exterior by the nephridiopores.

Podarke seems to be most similar to *Irma*. In both cases, the discharge of the genital products has been determined definitely to be by means of the ciliated organ and nephridium. In *Irma*, however, immature forms show the ciliated organ developing separately from the nephridium, the union taking place when the animal is sexually mature. In *Podarke* immature forms show the

[1] Treadwell, A. L., "Cytogeny of *Podarke obscura*," *Journal of Morphology*, 1900–1, Vol. 17.

[2] Goodrich, E. S., "On the Nephridia of the Polychæta," *Quarterly Journal of Morphology*, vol. 43, 1900.

ciliated organ and nephridium developing in union with one another. The form of the ciliated organ is also quite different from that of *Irma*. There is no resemblance to a "trumpet-shaped organ," the organ being in the form of a flat, triangular mass, as has already been stated, and is united at one point only, not entirely surrounding the nephridium as in *Irma*, yet the rolling of he dorsal and ventral edges may indicate an incomplete funnel.

Fage[1] has worked on these segmental organs in a number of forms in this family, and has found that in *Ophiodromus flexuosus*, *Oxydromus propinquus*, *Kefersteinia cirrata*, there is found a simple nephridium, slightly convoluted, opening to the exterior by a pore found in the region at the base of the parapodium, and into the body cavity by a straight nephrostome. At the moment of sexual maturity a ciliated organ formed from the peritoneum, is united with the nephridium and the sex products pass out through the compound organ. Goodrich did not observe this fact while working on the same forms.

In *Hesione pantherina*, the segmental organ is different, the excretory tube has many convolutions, the nephrostome is well developed possessing long cilia, the entire organ is much more highly modified than in other members of the family, and it closely resembles the excretory organ of the Lycoridea. At the time of sexual maturity, the organ undergoes no transformation. A ciliated organ homologous with that described in other forms of this group, is found near the nephrostome. It resembles the dorsal ciliated organ of *Nereis*. This organ develops at the same time as the nephridium and persists as an independent structure throughout the life of the individual. At its base is found the so-called phagocyte organ, containing in its meshes, granules comparable to the amœbocytes of the cœlome.

Thus we see that when the nephridium is highly developed and adapted more perfectly to its excretory function, it becomes more and more useless as a genital duct, and we find a special genital funnel appearing independent of the nephridium, and serving as a means of discharge for the sexual products. By this form, the family of Hesionidæ is closely connected with the family of Nereidæ.

[1] Fage, Louis, "Organes segmentaires des annelides Polychetes," *Annales des Sciences Naturelles*, Tome III., 1906.

Podarke obscura has been shown to possess a simple, uncoiled nephridial tube with a well differentiated ciliated organ developing at the same time and probably in union with the nephridium. No trace of a phagocyte organ was observed.

As a result of the investigations in this one family of the Polychætes, we may divide the Hesionidæ into three groups.

This classification is modeled somewhat after that made by Goodrich for the whole group of Polychæta. The nephridium has always an internal opening. Solenocytes have not been observed.

Group 1. — Forms in which the segmental organs consists of a nephridium highly differentiated, having a coiled tube and a well-developed nephrostome, and a distinct independent ciliated organ or genital funnel with an external opening through which the eggs are discharged. *Hesione pantherina.*

Group 2. — Forms in which the nephridium is a more simple tube opening into the cœlome by a small nephrostome. At the time of reproduction a ciliated organ is grafted on to the tube and affords a means of exit for the genital products. *Ophiodromus flexuosus, Oxydromus propinquus, Kefersteinia cirrata.*

Group 3. — Forms in which the nephridium is still more simple, having no coils. The nephrostome has been finally lost and its place taken by the ciliated organ or genital funnel, which develops at the same time, and probably in union with the nephridium. In this one group we may find forms illustrating the gradual loss of the nephrostome and the final fusion of the ciliated organ. *Hesione sicula, Tyrrhena, Irma, Podarke obscura.*

In this classification we have a gradual degeneration or modification of the nephridium from a condition where it performs its excretory function only, through a condition where it has become adapted temporarily to the secondary function of offering a means of sexual discharge to a condition finally where it has become so modified that from an early stage, if not throughout life, it functions as an excretory duct and a genital tube.

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